American Fern Journal 101(1):12–24 (2011)

Studies on the Gametophytes of Eight Chinese Species of *Dryopteris* (Dryopteridaceae)

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Abstract.—The gametophyte morphology and development of eight Chinese species of *Dryopteris* (Dryopteridaceae) were studied and described. Spores of all species were monolete and reniform. The germination pattern was the *Vittaria*-type. Germinal filaments were uniseriate, sometimes biseriate and the prothallial development was the *Aspidium*-type. Adult gametophytes in culture were cordiform, elongate-cordiform to cordiform-reniform, having wings with marginal and superficial trichomes. Gametangia belong to leptosporangiate fern type. Spore size, germination time, numbers of trichomes, morphology of rhizoids, formation time of the gametangia and gametophyte margin shape were different among the studied species.

Key Words.—*Dryopteris*, gametophytes, fern development

Dryopteris consists of about 230 species, which are distributed from temperate to tropical regions, with the highest species abundance and diversity in eastern Asia, especially in China (Li and Lu, 2006). Species in this genus are terrestrial with creeping rhizomes; petioles with numerous round, vascular bundles arranged in a ring; stems short–creeping to erect; leaves monomorphic, 1–3–pinnate-pinnatifid, gradually reduced distally to pinnatifid apex, herbaceous to somewhat leathery; pinnae not articulate to rachis; segment margins entire, crenate or serrate; sori round with a peltate indusium; spores brownish, coarsely rugose or with folded wings; and the chromosome number of x = 41 is common in the Dryopteridaceae.

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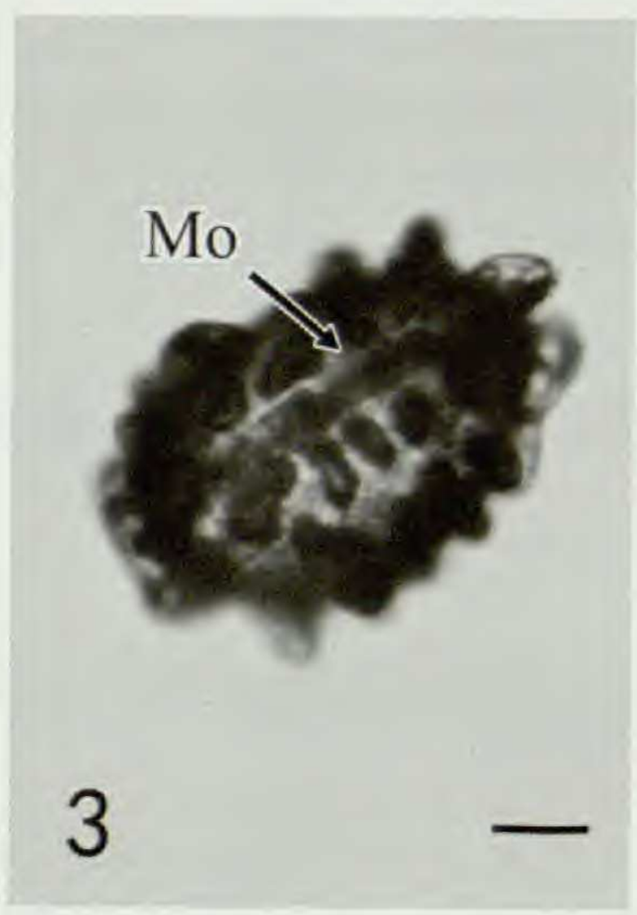
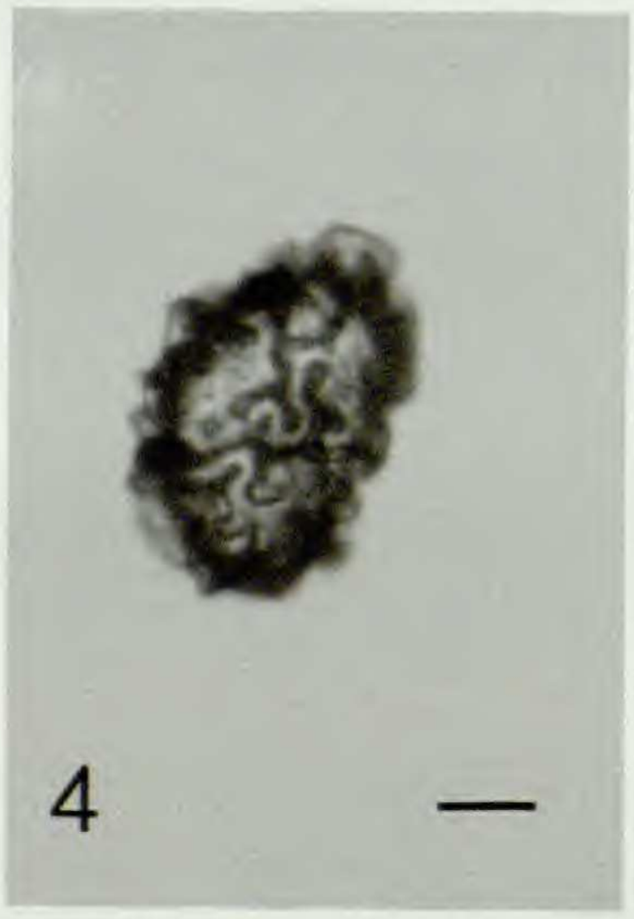
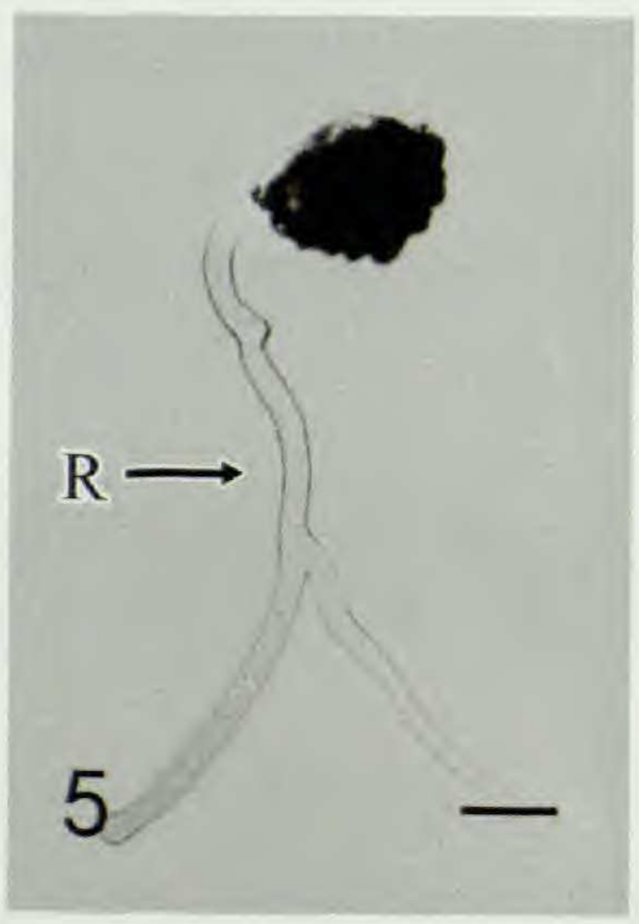
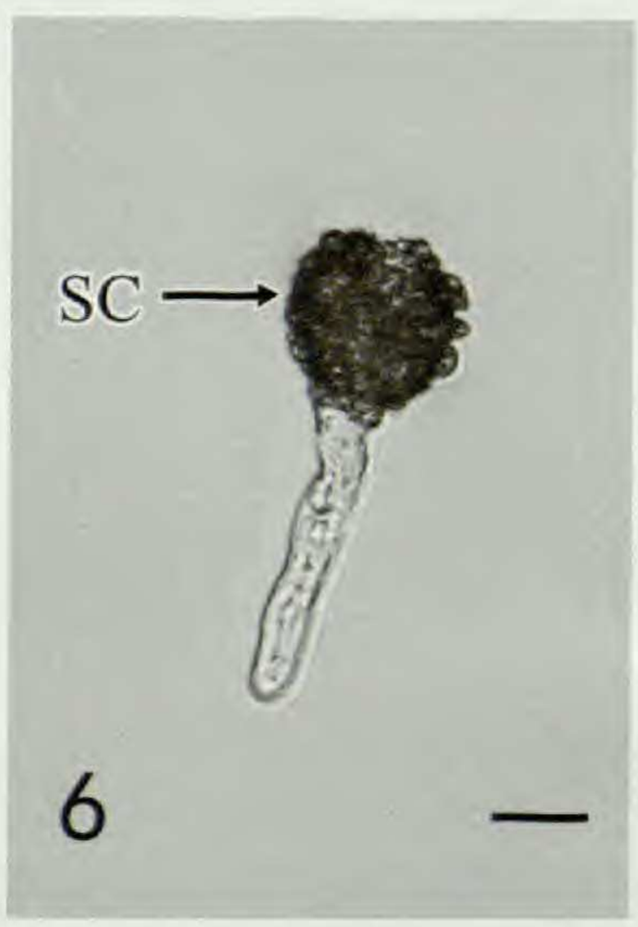
TABLE 1. Collection data.

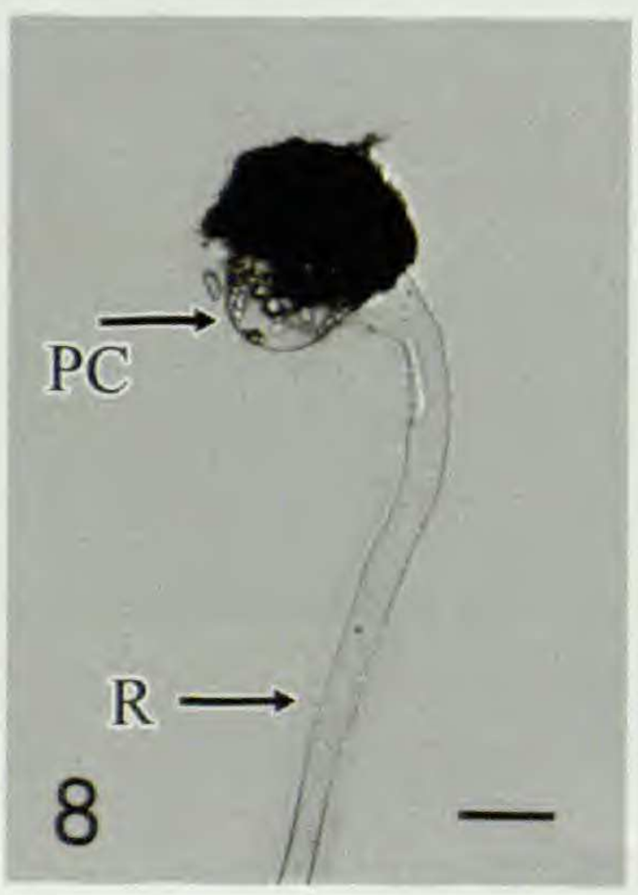
Dryopteris species	Collector name	Collection no. and date	Site location	Deposit herbarium	Spore numbers
D. expansa	X. C. Zhang	3079, 9/2003	Yunnan	Herbarium of Chinese National Herbarium, IBCAS (PE)	60
D. championii	X. C. Zhang	4142, 10/2006	Guangxi, Huaping	IBCAS (PE)	61
D. gymnosora	X. C. Zhang	4119, 10/2006	Guangxi, Huaping	IBCAS (PE)	60
D. indusiata	X. C. Zhang	4145, 10/2006	Guangxi, Huaping	IBCAS (PE)	60
D. subtriangularis	X. C. Zhang	3083, 09/2003	Yunnan, Pingbian	IBCAS (PE)	59
D. fructuosa	X. C. Zhang	2749, 09/2002	Sichuan, Panzhihua	IBCAS (PE)	60
D. atrata	X. Cheng	2011, 01/2000	Yunnan, Kunming	Herbarium of Kunming Institute of Botany, CAS (KUN)	60
D. integriloba	B. D. Liu	567, 12/2004	Hainan, Wuzhishan	Herbarium of Harbin Normal Univeristy	60











FIGS. 1–9. Spore morphology, germination and filamentous phase of *Dryopteris*. 1. Spore of *D. gymnosora*; scale bar = 20 μm. 2. Spore of *D. indusiata*; scale bar = 15 μm. 3 Spore of *D. subtriangularis* with monolete (Mo) scar (arrow); scale bar = 15 μm. 4. Spore of *D. integriloba*; scale bar = 15 μm. 5. Germination of *D. fructuosa* with rhizoid (R); scale bar = 22 μm. 6. Germination of *D. indusiata* with spore coat (SC); scale bar = 15 μm. 7. Germination of *D. championii*; scale bar =

Although much taxonomical and systematic research on the genus *Dryopteris* has been performed (Tryon and Tryon, 1982; Kramer and Green, 1990; Geiger and Ranker, 2005) and the Chinese taxa have been described (Ching, 1965, 1978; Li and Lu, 2006; Liu *et al.*, 2007), the relationships among *Dryopteris* species remain poorly understood. Since gametophyte morphology of ferns is considered to be significant and characteristic of fern taxa (Chen *et al.*, 2008), studies on the gametophytes of *Dryopteris* species should be performed.

Gametophyte morphology and development of several *Dryopteris* species have been studied and summarized (Cousens, 1975; Cousens and Horner, 1970; Duncan, 1943; Kanamori, 1967; Kaur, 1977; Loyal, 1959; Momose, 1937, 1939; Pérez-García *et al.*, 1999, 2001). However, there have been no detailed reports on several species of *Dryopteris*. Hence, this paper describes the morphogenetic study of *D. atrata* (Wall) Ching, *D. championii* (Benth.) C. Chr., *D. expansa* (C. Presl) Fraser-Jenk. & Jermy, *D. gymnosora* (Makino) C. Chr., *D. fructuosa* (Christ) C. Chr., *D. indusiata* Makino & Yamam, *D. integriloba* C. Chr., *D. subtriangularis* (C. Hope) C. Chr.

Materials and Methods

Materials for research were obtained from several China localities (Table 1). Spores were collected from fertile pinnae of eight different living plants (*Dryopteris atrata*, *D. championii*, *D. expansa*, *D. gymnosora*, *D. fructuosa*, *D. indusiata*, *D. integriloba*, and *D. subtriangularis*) and leaves with spores were kept in clean paper bags under dry conditions. The remains of sporangia and indusia were eliminated by a mesh with pores 0.054 mm in diameter one week later. Spores were spread evenly in plastic basins (measuring 25 cm × 20 cm × 5 cm) with a sieved mixture of black soil and sand (Zhang *et al.*, 2008) at an average density of 100–150 spores per cm^2. Basins were covered with transparent plastic film to avoid contamination and desiccation, under a diurnal cycle of 12/12 hr, with fluorescent light (10,000 $\mu mol \cdot m^{-2} \cdot sec^{-1}$), at 25 °C.

Spore sizes were measured from material in water with a compound microscope (No. XTS 20130, Beijing Tech Instrument Co., LTD) equipped with an ocular micrometer. An average of sixty measurements of the spore length and width per species were made. Spore morphology was observed under the compound microscope from material in water.

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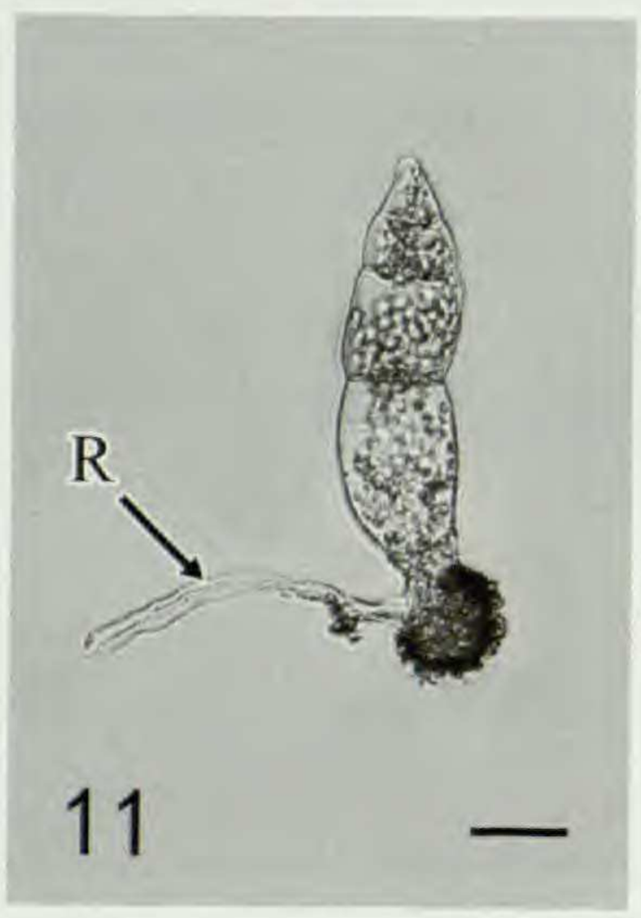
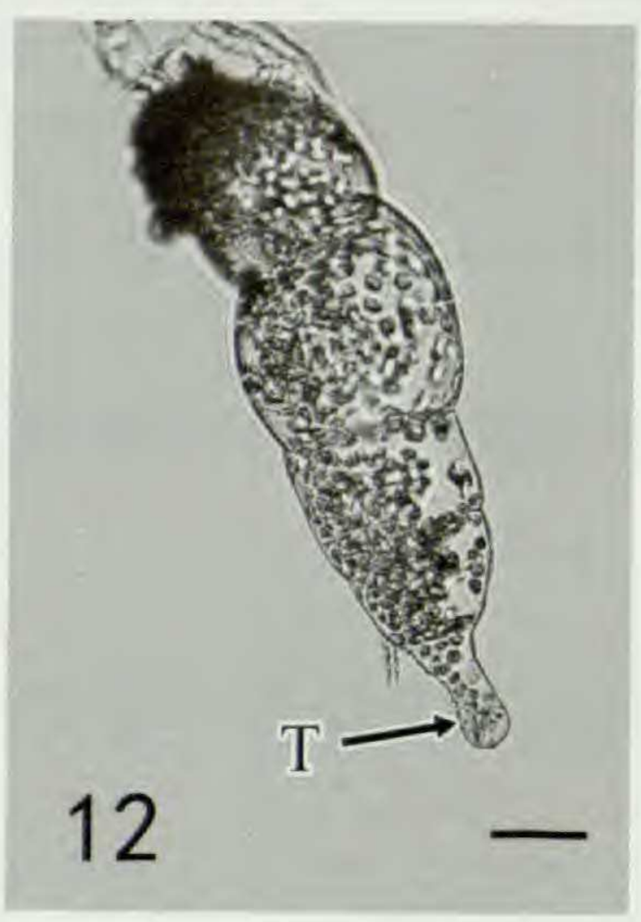
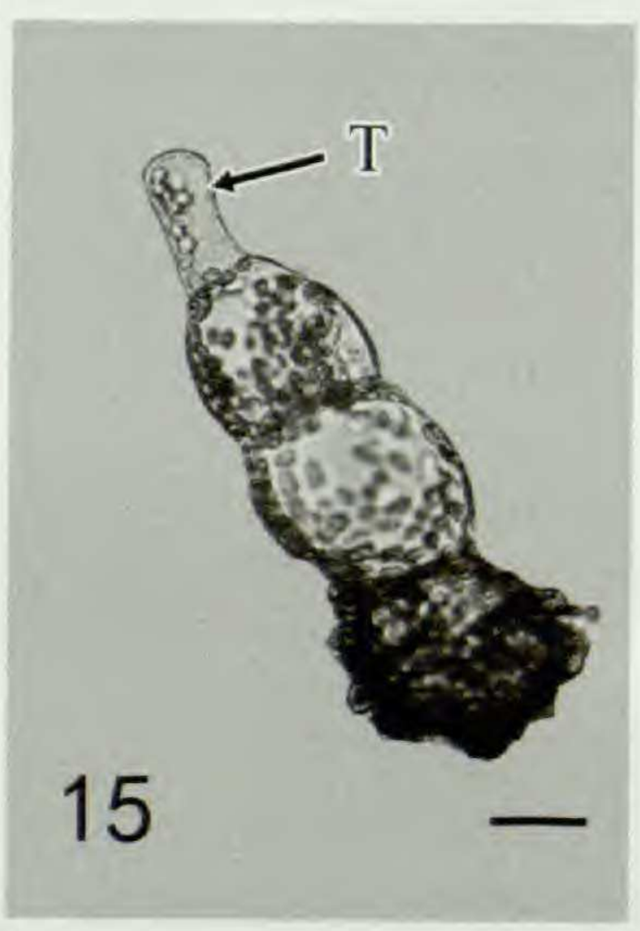
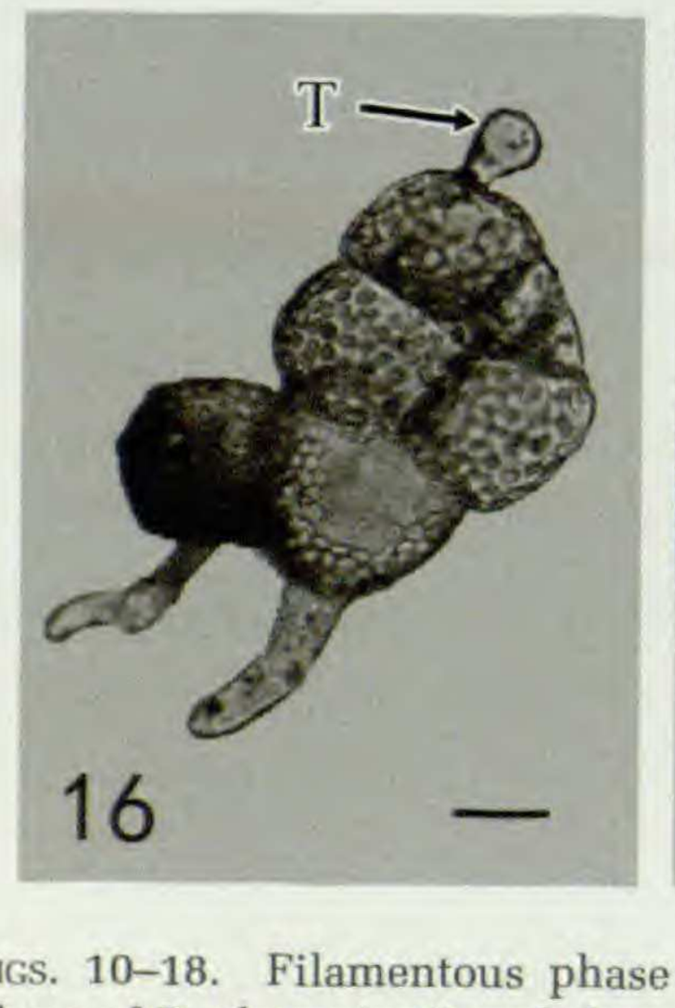
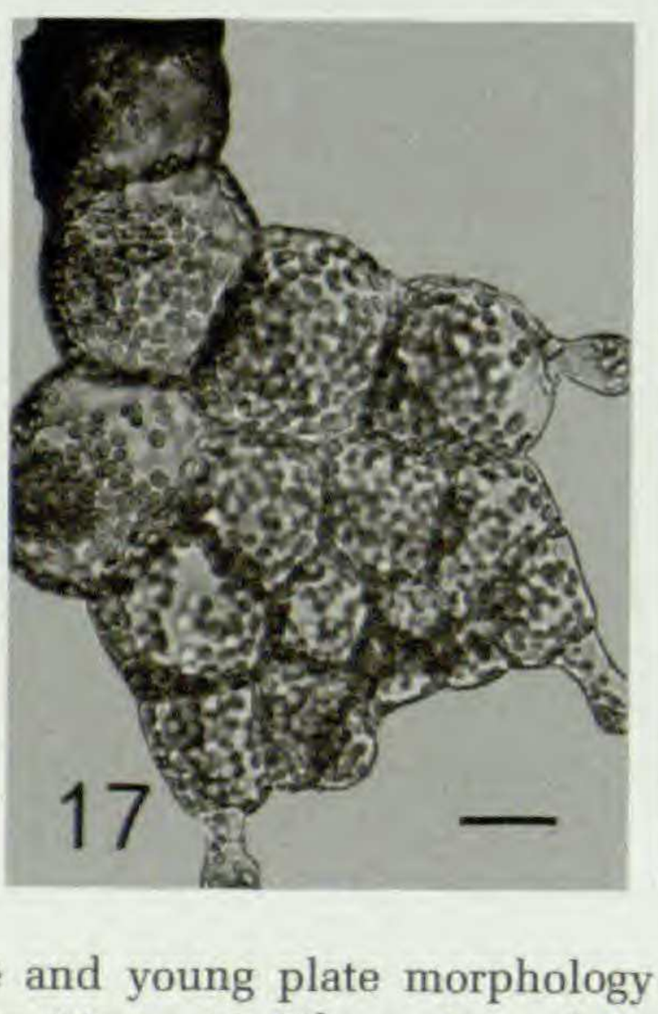
30 μm. 8. Germination of *D. fructuosa* with prothallial cell (PC); scale bar = 25 μm. 9. Filamentous phase of *D. gymnosora* with a trichome (T); scale bar = 40 μm.

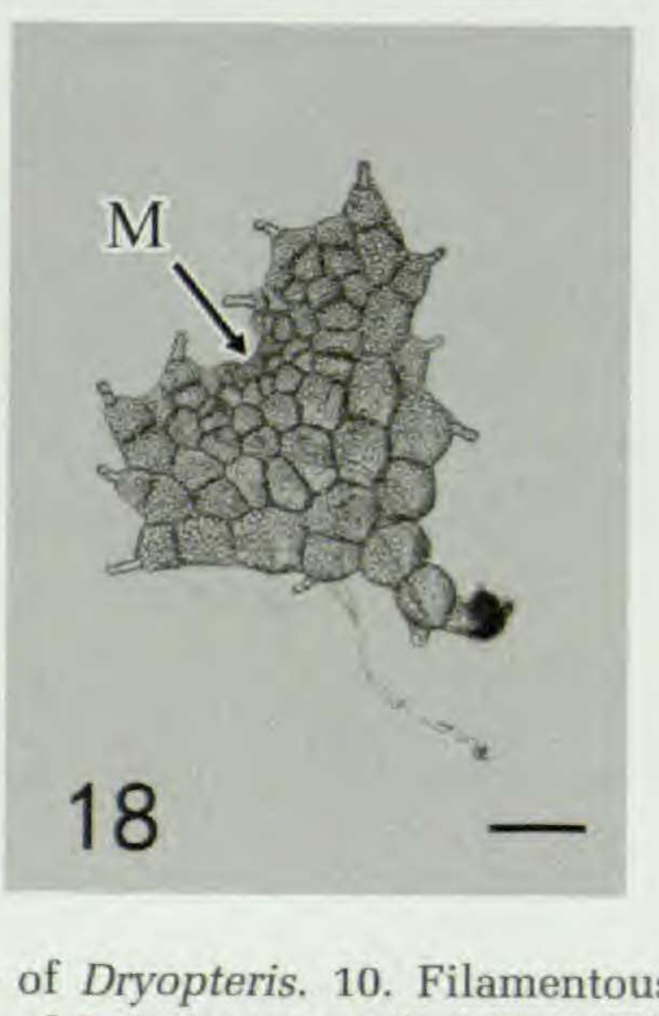












FIGS. 10–18. Filamentous phase and young plate morphology of *Dryopteris*. 10. Filamentous phase of *D. championii*; scale bar = 30 μm. 11. Filamentous phase of *D. indusiata* with rhizoid (R); scale bar = 30 μm. 12. Filamentous phase of *D. championii* with trichome (T); scale bar = 30 μm. 13. Biseriate Filament of *D. subtriangularis*; scale bar = 60 μm. 14. Filamentous phase of *D. atrata*; scale bar = 30 μm. 15. Filamentous phase of *D. subtriangularis* with trichome (T); scale bar =

Results

Spores.—Spores of all species were homosporous, reniform and monolete. Size was variable among species. Spore measures were (21) 24 (30) × (31) 36 (40) μm in *D. expansa*, (25) 29 (33) × (50) 55 (60) μm in *D. championii*, (36) 40 (45) × (61) 72 (83) μm in *D. gymnosora*, (27) 32 (36) × (51) 60 (62) μm in *D. indusiata*, (60) 65 (70) × (100) 112.5 (120) μm in *D. subtriangularis*, (29) 32 (34) × (32) 40 (45) μm in *D. fructuosa*, (28) 31 (36) × (42) 46 (49) μm in *D. atrata* and (29) 33 (36) × (33) 38 (43) μm in *D. integriloba* (Figs. 1–4). Perine was winged (Tryon and Lugardon, 1991).

Germination.—The germination rate in spores was 90%. The germination process began after about 20 days in *D. expansa*, 7–12 days in *D. championii*, about two weeks for *D. gymnosora*, 8–11 days for *D. indusiata*, about one week for *D. subtriangularis*, about 25 days for *D. fructuosa*, about 20 days for *D. atrata* and about 24 days for *D. integriloba*. All the species share *Vittaria*-type (Nayar and Kaur, 1971) germination after sowing (Figs. 5–7). The short and hyaline rhizoid appeared first and initially had a wall perpendicular to the polar axis, and was followed by the first prothallial cell (Fig. 8). The initial prothallial cell was characterized by a large number of chloroplasts.

Filamentous phase.—In most species, with the division of the first prothallial cell by a transverse wall, an apical cell was produced, and finally a uniseriate germ–filament formed, which was 2–20 cells long (Figs. 9–12). Cells were barrel–shaped and had abundant chloroplasts. However, in *D. subtriangularis*, the germ-filament was uniserial or biseriate (Fig. 13). In *D. atrata*, there were two types of germ-filament: uniseriate and branched (Fig. 14). The germ–filament developed an apical unicellular trichome in the early phases of gametophyte development, which was observed in *D. gymnosora*, *D. indusiata* and *D. subtriangularis* (Figs. 9, 11, 12, 15). In *D. championii*, *D. expansa*, *D. atrata* and *D. fructuosa*, trichomes formed in the laminar phase. Compared with the other species, trichomes were produced earliest in *D. subtriangularis* when the germ-filament was only 2 cells long (Fig. 15). The spore coat remained attached.

Laminar phase.—The differentiation of the laminar phase was asynchronous and development occurred between days 17 (*D. championii*) and 41 (*D. gymnosora*). In *D. subtriangularis*, although the terminal cell of the germ-filament had produced a trichome, it still took part in the laminar formation. It divided longitudinally into a larger and a smaller cell. The larger one remained inactive and the smaller one divided actively, contributing to the development of the prothallial plate (Fig. 16). As a result, the plate was slightly lopsided at the anterior end (Fig. 17). A meristematic cell was differentiated in one of the

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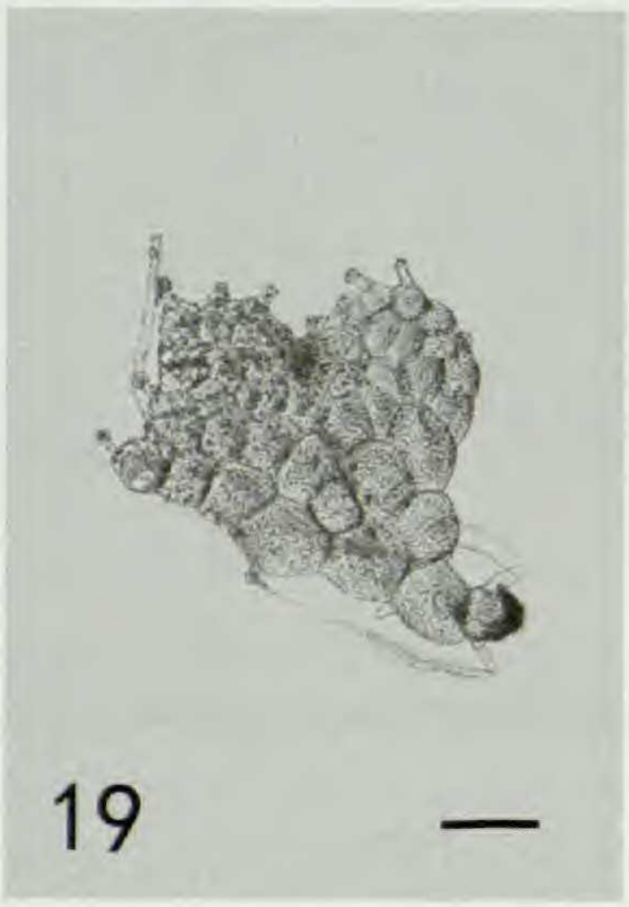
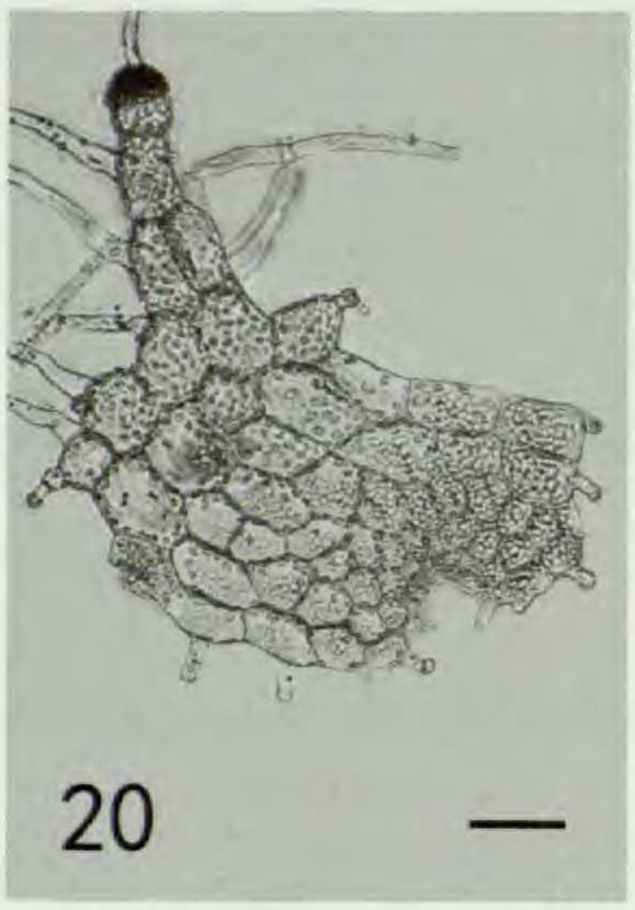
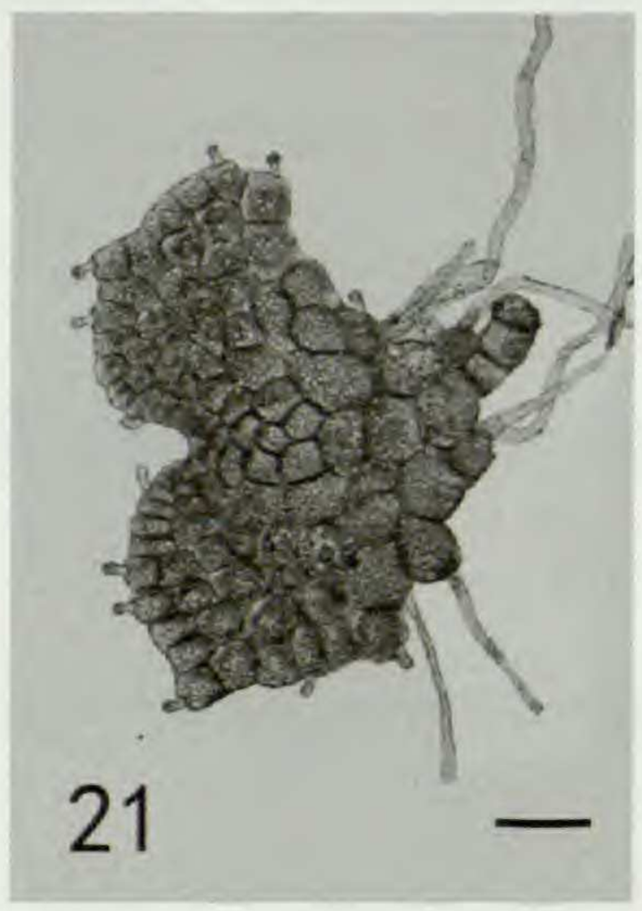
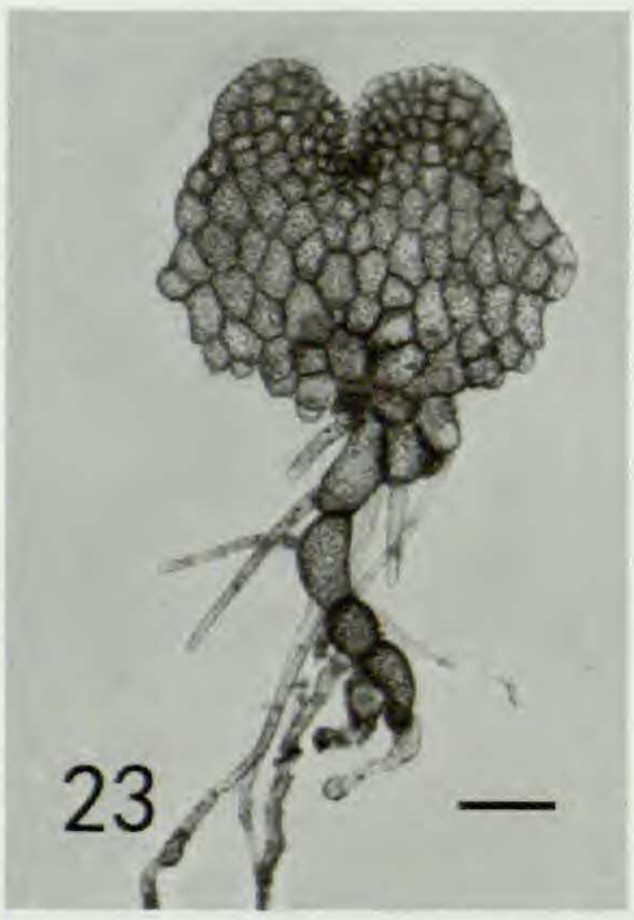
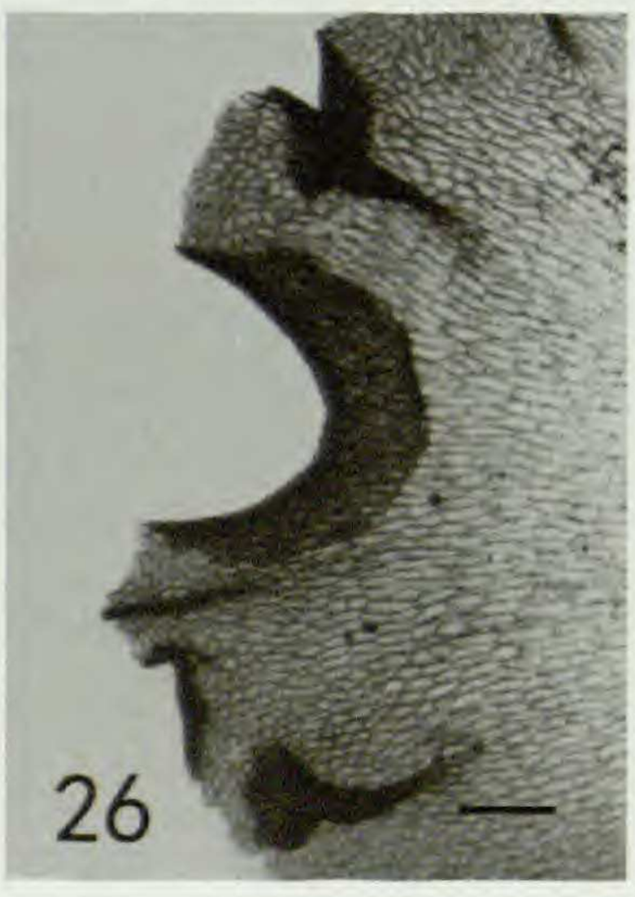
35 μm. 16. Filament develops towards prothallial plate stage of *D. subtriangulari* with trichome (T); scale bar = 35 μm. 17. Plate phase of *D. subtriangularis*; scale bar = 35 μm. 18. Young gametophyte of *D. championii* with meristem (M); scale bar = 60 μm.

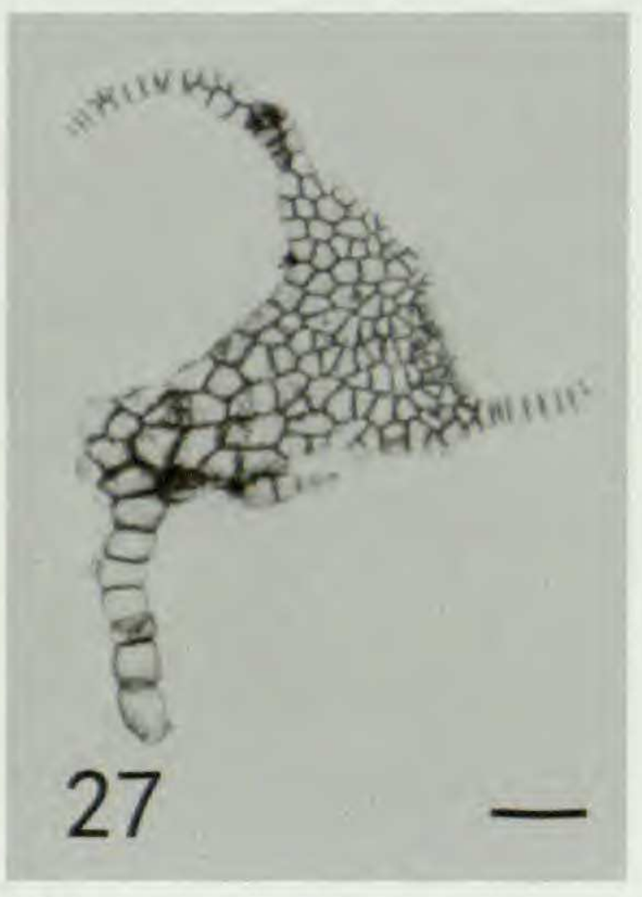












FIGS. 19–27. Plate phase of *Dryopteris*. 19. Young plate of *D. gymnosora*; scale bar = 80 μm. 20. Gametophyte of *D. indusiata*; scale bar = 60 μm. 21. Gametophyte of *D. subtriangularis*; scale bar = 200 μm. 22. Mature gametophyte of *D. atrata*; scale bar = 70 μm. 23. Young gametophyte of *D. expansa*; scale bar = 120 μm. 24. Cordiform gametophyte of *D. expansa*; scale bar = 150 μm. 25. Mature gametophyte of *D. expansa*; scale bar = 150 μm. 26. Gametophyte with folded margins of *D. expansa*; scale bar = 350 μm. 27. Diverse plate phase of *D. fructuosa*; scale bar = 150 μm.

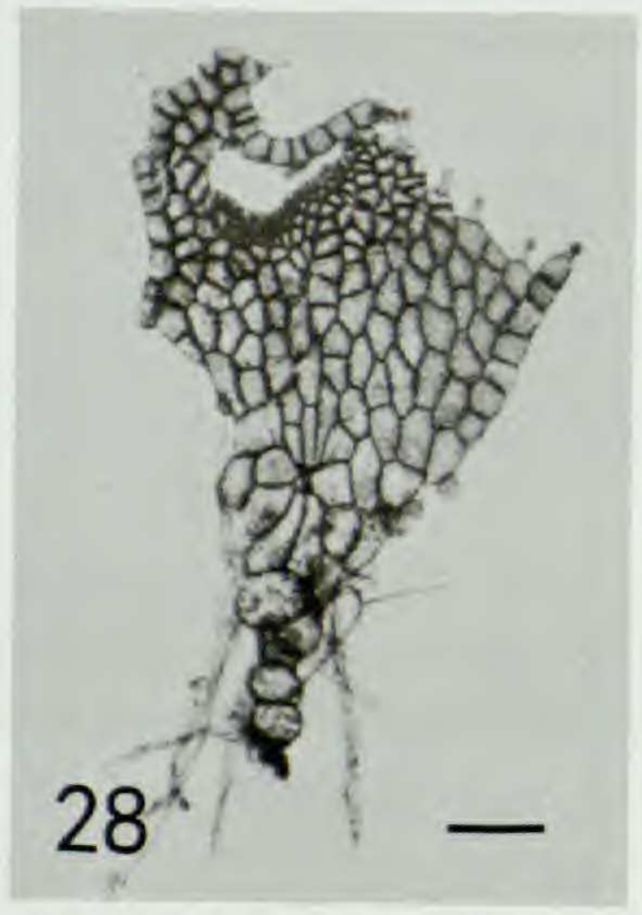
marginal cells formed from the active smaller cell. Prothallial development in all species was *Aspidium*-type (Nayar and Kaur, 1969).

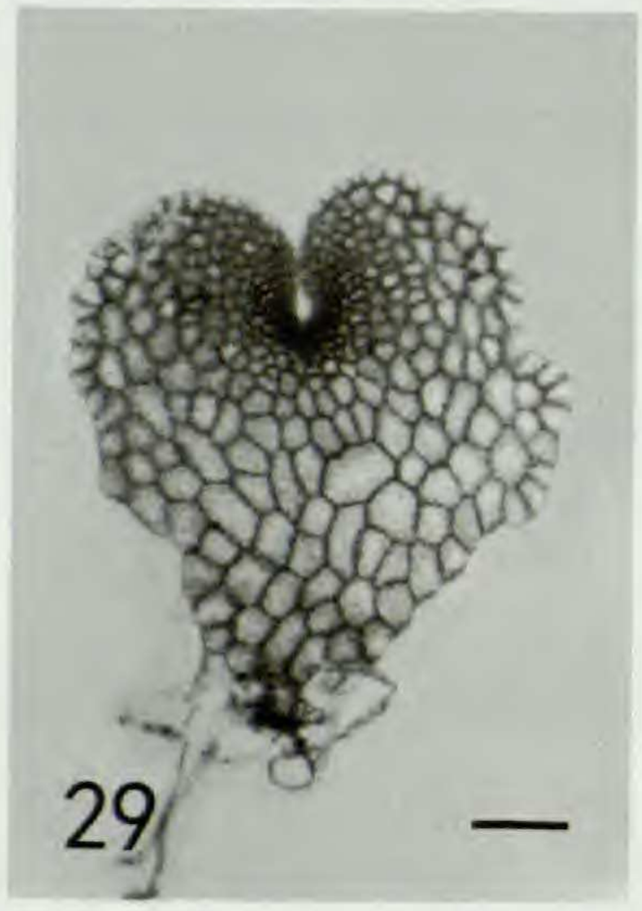
Young gametophytes of *D. championii* were cordiform-spatulate, becoming cordiform with age, with underdeveloped wings and irregular margins (Fig. 18). The young plate phase of *D. gymnosora* was cordiform-reniform (Fig. 19), but at maturity was mostly cordiform, with strongly developed wings and smooth to slightly irregular margins. Gametophytes in *D. indusiata* and *D. subtriangularis* were spatulate when young and cordiform when mature (Figs. 20–21), with wide wings and smooth to slightly irregular margins. Young gametophytes of *D. atrata* were spatulate with very irregular margins and filamentous extensions 2–6 cells long. When mature they became cordiform-reniform with well–developed wings (Fig. 22). Gametophytes in *D. expansa* were spatulate when young, becoming cordiform to cordiform-reniform when mature, with smooth to irregular margins (Figs. 23–25). Folded margins were observed in some gametophytes (Fig. 26). Gametophytes in *D. fructuosa* were the most variable: they were irregular spatulate with small extensions when young (Fig. 27), and when mature they were elongate-cordiform, with irregular margins with filamentous extentions 3–20 cells long, or plate extensions 10–30 cells long (Fig. 28). Sometimes cordiform-reniform gametophytes with irregular margins developed (Fig. 29). Gametophytes in *D. integriloba* were spatulate when young and cordiform to cordiform-reniform when mature, with wide wings and smooth to slightly irregular margins (Fig. 30).

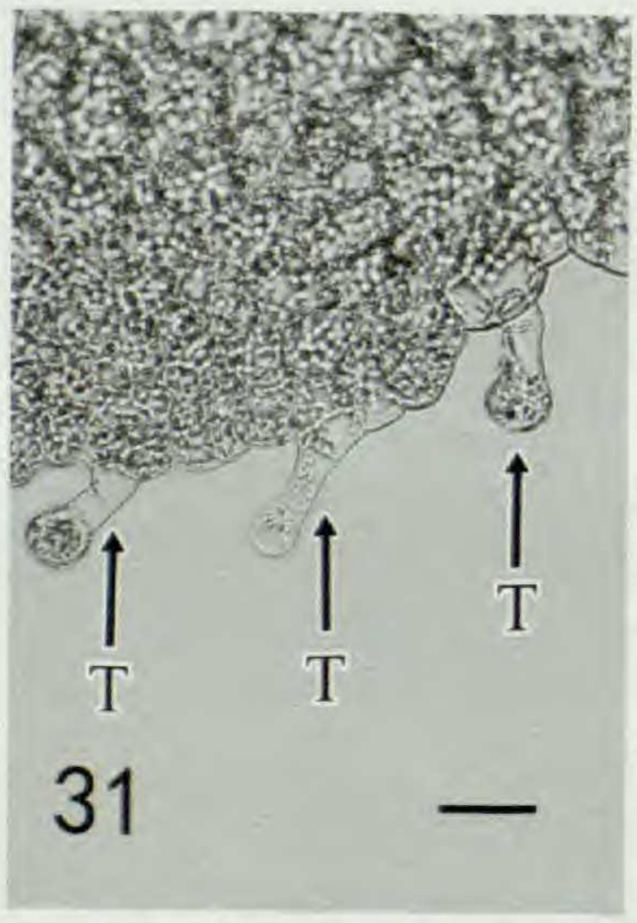
Adult gametophyte.—The time for the first adult gametophytes of all species to differentiate varied from days 21 (*D. subtriangularis)* to 52 (*D. fructuosa*). Under our cultural conditions, the largest adult gametophyte belonged to *D. subtriangularis* (7 × 4 mm).

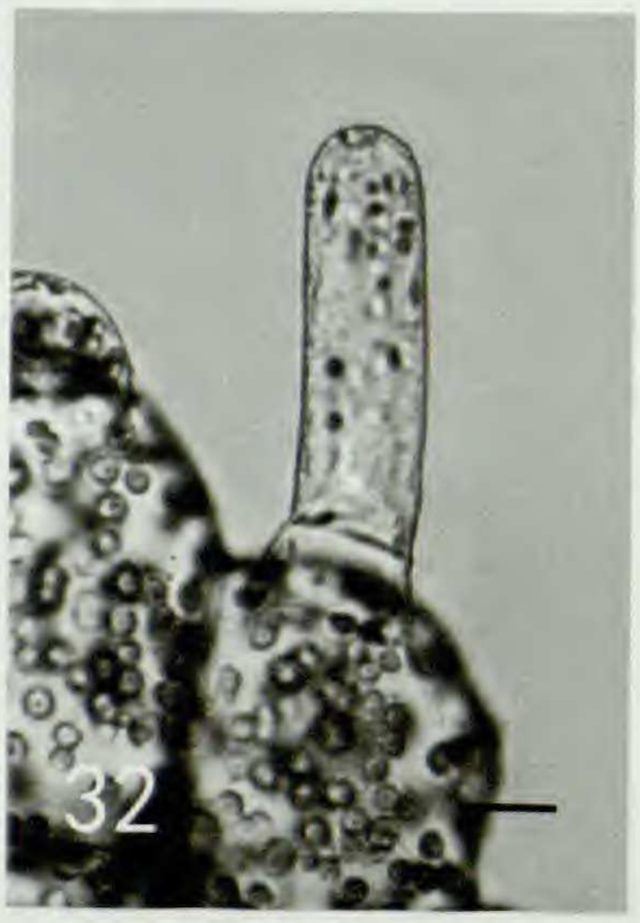
For most species, the first trichome originated from the terminal cell of the filament. With the development of the gametophyte, more and more trichomes were produced by division of the other prothallial cells. Trichomes were found on the margin and surfaces of the gametophytes, and were papillate to slender claviform, with or without glands (Figs. 31–32). They were most abundant in gametophytes of *D. subtriangularis* at an average of 100 (Fig. 33), compared with those of *D. indusiata* (11), *D. gymnosora* (23), *D. championii* (12), *D. expansa* (26), *D. atrata* (20), *D. fructuosa* (17), and *D. integriloba* (10). Chloroplasts were mainly distributed at the apex of the trichome, which are generally smaller in size compared to those of other prothallial cells. Chloroplasts in the marginal cells were mostly disk-shape and in the central cells were oval, disk-shape and dumbbell-shape (Fig. 34). Some marginal cells connecting to trichomes were prominent.

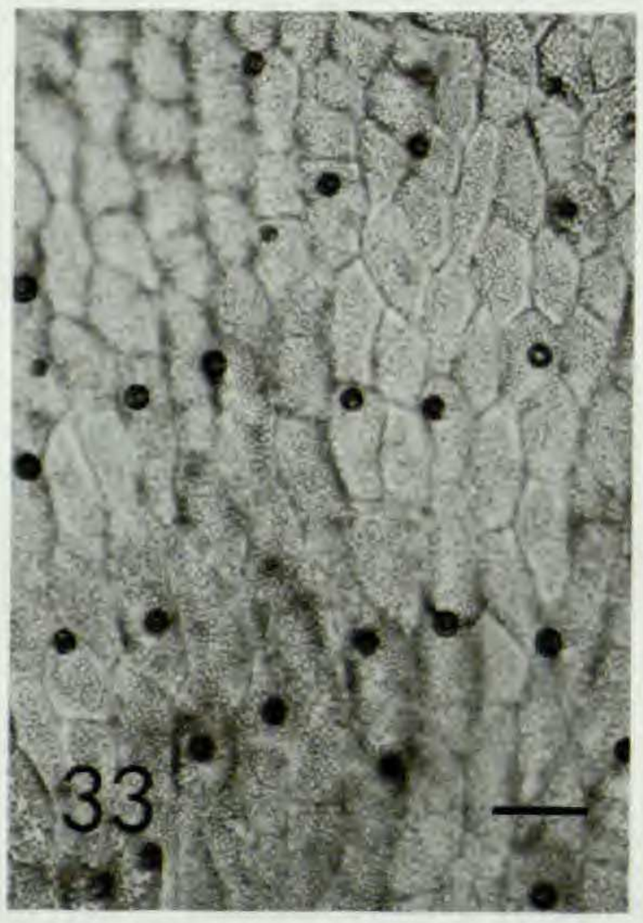
Rhizoids were formed by the cell divisions of the prothallial cells. In all species, the first rhizoids were hyaline. With the development of the prothallus, the rhizoids of all species became brown and curved. Rhizoids developed mainly on the ventral surface of the young prothallus but they also could be observed on the mature prothallial margins.

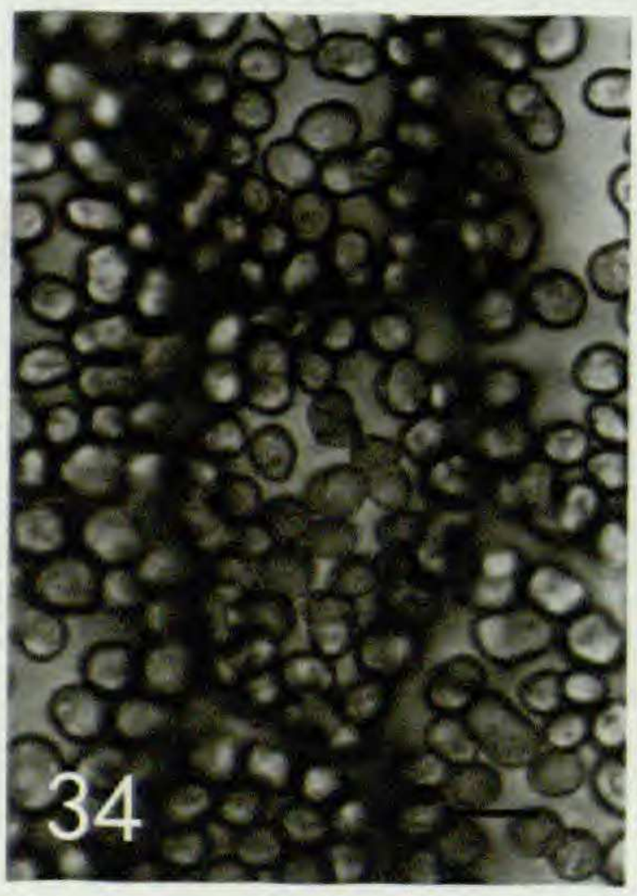


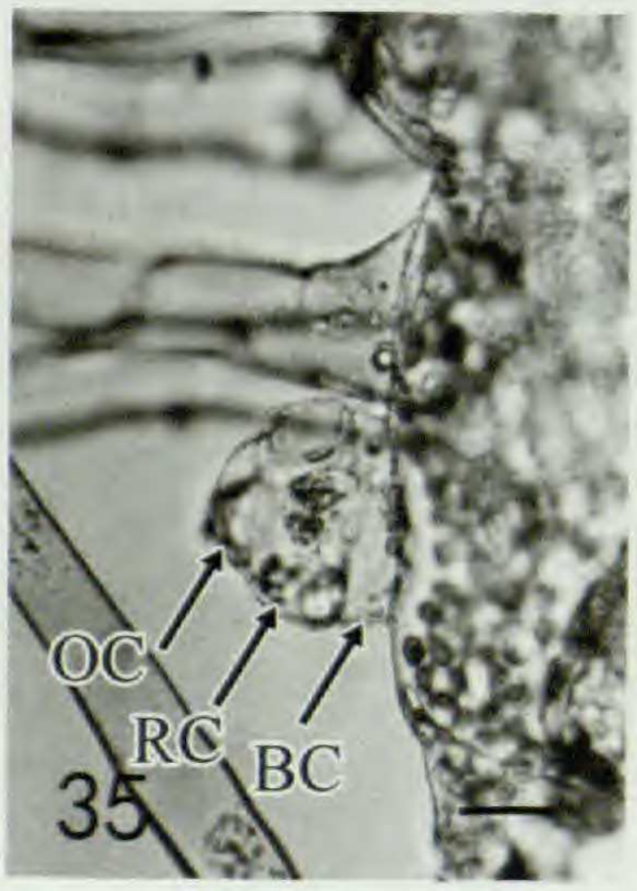


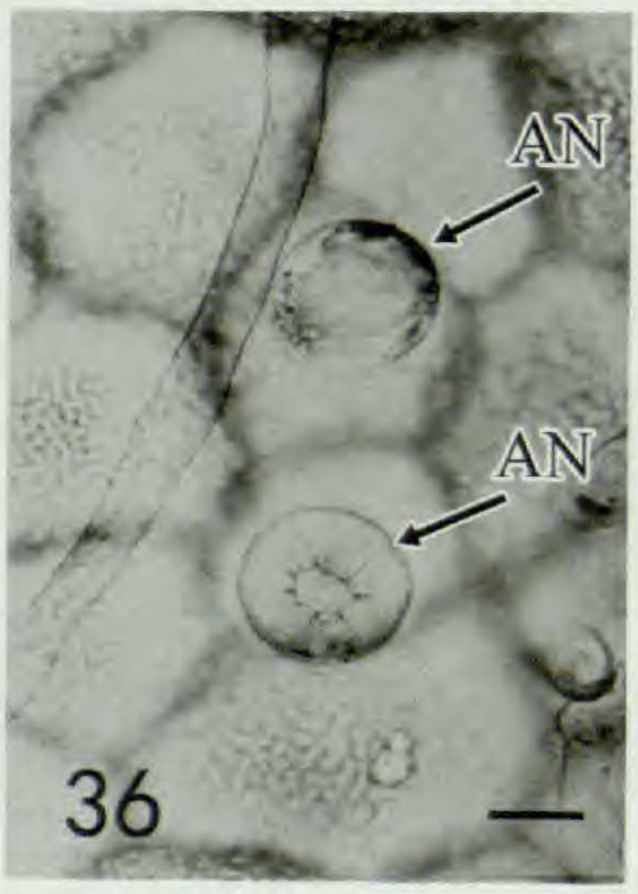












FIGS. 28–36. Gametophyte morphology, trichome, and antheridia of *Dryopteris*. 28. Diverse prothallium phase of *D. fructuosa*; scale bar = 150 μm. 29. Cordiform-reniform gametophyte of *D. fructuosa*; scale bar = 150 μm. 30. Gametophyte of *D. integriloba*; scale bar = 150 μm. 31. Trichomes (arrows) of *D. gymnosora*; scale bar = 100 μm. 32. Trichome of *D. fructuosa*; scale bar = 30 μm. 33. Distribution of the trichomes on the mature prothallus of *D. subtriangularis* (The black

Gametangia.—The gametophytes are sexually mature once the gametangia form. Time for gametangia formation varied from 25 days in *D. indusiata* to 80 days in *D. gymnosora*. The antheridia were restricted to the basal part of the gametophyte (between the rhizoids). The number of the antheridia varied from 10–40 per gametophyte. Morphologically, the antheridia were globose, and consisted of a basal cell, an annular or ring cell and an opercular cell (Fig. 35). Antherozoids were liberated by detachment of the operculum (Fig. 36).

The archegonia developed on the cushion near the meristematic zone of the gametophyte. Their necks were elongated, composed of 3–5 tiers of cells with each tier having four cells. The archegonia became brown when they were post-mature (Figs. 37).

Sporophytes.—The first sporophytes were observed by about 8–12 weeks after sowing. In all species, the first leaves were spatulate, bilobed to trilobed (Fig. 38). Fertilization occurred on almost all gametophytes to produce sporophytes (Fig. 39).

Discussion

The spores of all species shared features such as monolete spores and ornamented perine. However, the spore sizes of the studied species were different.

Germination times differed in the different species, corresponding with previous studies for other species of Dryopteridaceae (Chandra and Nayar, 1970; Mendoza *et al.*, 1999a, 1999b, 2002; Pérez-García *et al.*, 1999, 2001; Mendoza and Pérez-García, 2003; Mendoza, 2001). The germination pattern in all species was of the *Vittaria*-type, as observed by Nayar and Kaur (1971), Chandra and Nayar (1970), Mendoza *et al.* (1999a, 1999b, 2002, 2003), Pérez-García *et al.* (1999, 2001), Mendoza (2001) in Dryopteridaceae. It is the most common type in ferns. In this type, the rhizoid develops first after the formation of a wall perpendicular to the polar axis of the spores (Nayar and Kaur, 1971).

Germinative uniseriate filaments were 2–10 cells long in all species. Biseriate filaments in *D. subtriangularis* were 4–12 cells long in our cultural conditions. Uniseriate and branched germ–filaments appeared in *D. atrata*. The prothallial development was *Aspidium*–type, which is also observed by Pérez–García *et al.* (1999, 2001) for *Dryopteris* species in Mexico. In this type, the apical cell of the germ–filament produced a unicellular papillate trichome crowning it. Commonly, the apical cell becomes sluggish. However, in some cases, this cell remains active and divides, taking part in prothallial plate formation (Nayar and Kaur, 1971). The prothallial development of the studied

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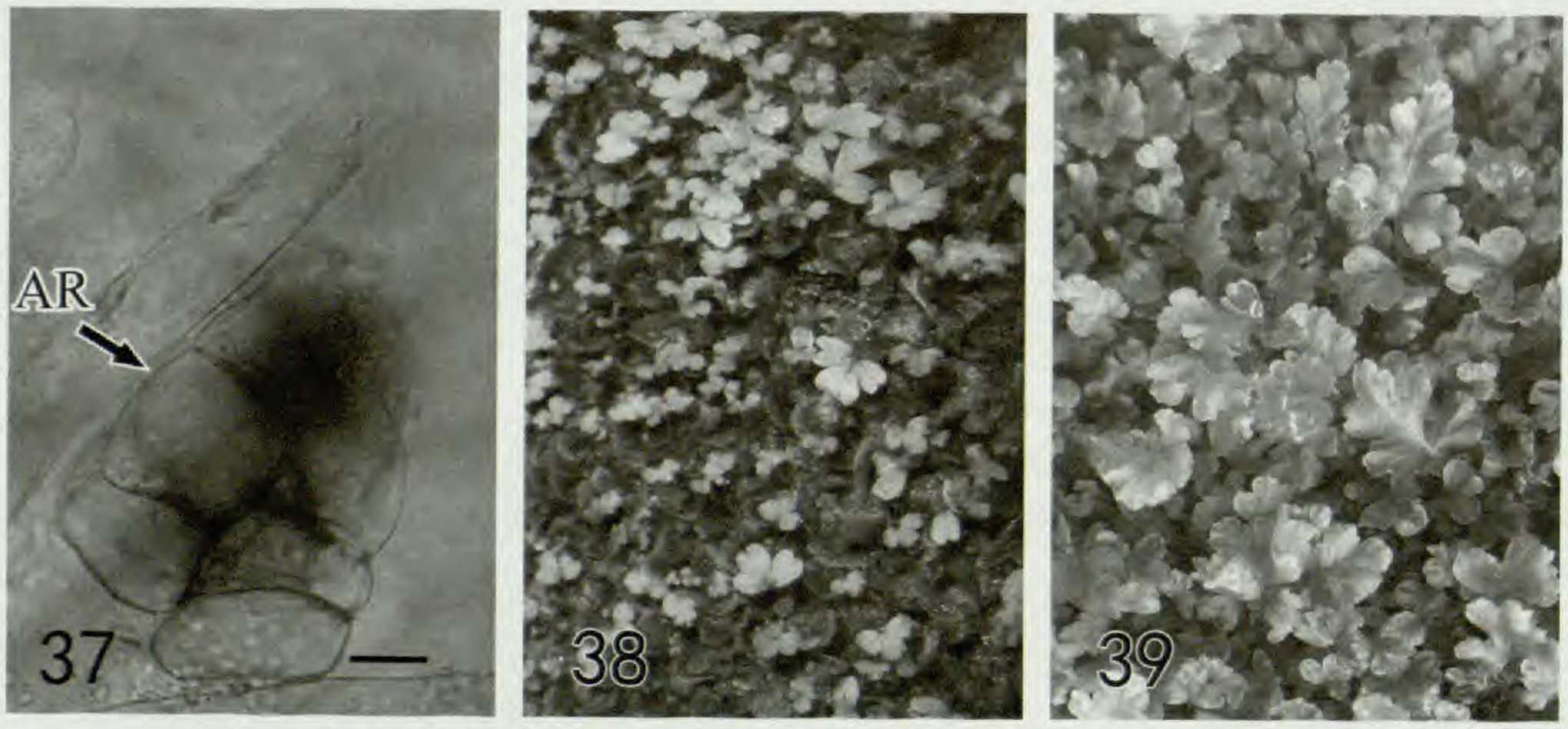
spots show the trichomes); scale bar = 500 μm. 34. Prothallial cells showing the chloroplasts of *D. fructuosa*; scale bar = 15 μm. 35. Antheridia of *D. integriloba* with basal cell (BC), ring cell (RC) and opercular cell (OC); scale bar = 30 μm. 36. Antheridia (arrows) of *D. atrata*; scale bar = 30 μm.



FIGS. 37–39. Archegonia and sporophyte of *Dryopteris*. 37. The lateral view of the mature archegonium (arrow) of *D. subtriangularis*; scale bar = 10 μm. 38. Young sporophytes of *D. gymnosora*. 39. Young sporophytes of *D. subtriangularis*.

species occurred according to the latter route. The adult gametophyte developed faster in *D. subtriangularis* than in the other species.

Trichomes of all studied taxa were papillate to slender claviform, with or without glands, contrasting with the observations of Pérez–García *et al.* (1999, 2001), who noted that trichomes of *Dryopteris* are unicellular, capitate rounded apex, with a layer of extracellular secretion. Trichomes were found on the margin and surfaces of the gametophytes, agreeing with the observations by Pérez–García *et al.* (1999, 2001) for other species of *Dryopteris*.

The observed morphology supports the description of Pérez–García *et al.* (1999, 2001), who found that gametophytes of the genus *Dryopteris* are spatulate, cordiform-spatulate, reniform, or cordate.

Sex organs of the studied taxa are of the typical leptosporangiate type, similar to the description of Dryopteridaceae given by Nayar and Kaur (1971).

The rhizoids in all species developed on the ventral surface and margin of the prothallus; they were initially hyaline and subsequently became brown in mature and older prothallia. Nevertheless, differences in the morphology of the rhizoids in some species were observed. Furthermore, number and length of the rhizoids in all species were different.

The *Vittaria*-type germination, the *Aspidium*–type prothallial development, the presence of unicellular trichomes, and the morphology of the adult gametophytes, are diagnostic characteristic features for the genus *Dryopteris*. Distinguishing features among the studied species are size of the spores, germination time, time of formation of the gametangia, and thallus margin shape.

ACKNOWLEDGMENTS

This work was supported by National Natural Science Foundation of China (30973876), the Project of Chinese Academy of Sciences (CZBZX-1), High-Tech Research and Development

Program of China (HTRDP) 863 (2007AA021405), Jiangsu Planned Projects for Postdoctoral Research Funds (1001078C) and China Postdoctoral Science Foundation funded project (20100481152). We would like to thank Dr. Aniceto Medoza-Ruiz and Dr. X. C. Zhang for valuable comments on the manuscript. We also thank Dr. X. Cheng for his help in the collection of *Dryopteris* spores.

Literature Cited

Chandra, P. and B. K. Nayar. 1970. Morphology of some polystichoid ferns. I. The gametophytes of *Arachniodes*, *Cyrtomium* and *Polystichum*. Bot. J. Linn. Soc. 63:265–276.

Chen, G. J., X. Cheng, B. D. Liu and Y. Jiao. 2008. Comparative studies on gametophyte morphology and development of seven species of Cyatheaceae. Amer. Fern J. 98:83–95.

Ching, R. C. 1965. Dryopteridaceae–a new fern family. Acta Phytotax. Sin. 10:1–5.

Ching, R. C. 1978. The Chinese fern families and genera: systematic arrangement and historical origin. Acta Phytotax. Sin. 16:1–59.

Cousens, M. I. 1975. Gametophyte sex expression in some species of *Dryopteris*. Amer. Fern J. 60:13–27.

Cousens, M. I. and H. T. Horner. 1970. Gametophyte ontogeny and sex expression in *Dryopteris ludoviciana*. Amer. Fern J. 60:13–27.

Duncan, R. E. 1943. Origin and development of embryos in certain apogamous forms of *Dryopteris*. Bot. Gaz. 105:202–211.

Geiger, J. M. O. and T. A. Ranker. 2005. Molecular phylogenetics and historical biogeography of Hawaiian *Dryopteris* (Dryopteridaceae). Mol. Phylogenet. Evol. 3:392–407.

Kanamori, K. 1967. Origin and early development of apogamous embryos in the prothallia of *Dryopteris chinesis*. J. Jap. Bot. 42:111–118.

Kaur, S. 1977. Morphology of the prothallus and juvenile sporophytes of some species of *Dryopteris*. Proc. Indian Acad. Sci. 85:163–171.

Kramer, K. U. and P. S. Green. 1990. Pteridophytes and gymnosperms. Pp. 74–80. *In:* The families and genera of vascular plants, K. Kubitzki, (ed.). Springer–Verlag, Berlin.

Li, C. X. and S. G. Lu. 2006. Phylogenetics of Chinese *Dryopteris* (Dryopteridaceae) based on the chloroplast *rps*4-*trn*S sequence data. J. Plant Res. 119:589–598.

Liu, H. M., X. C. Zhang, W. Wang, Y. L. Qiu and Z. D. Chen. 2007. Molecular phylogeny of the fern family Dryopteridaceae inferred from chloroplast *rbc*L and *atp*B genes. Int. J. Plant Sci. 689:1311–1323.

Loyal, D. S. 1959. Some observations on the cytology and apogamy of Himalayan *Dryopteris paleacea* (Don.) Hand. Mazz. J. Indian Bot. Soc. 39:608–613.

Mendoza-Ruiz, A. 2001. *Morfogénesis de la fase sexual de pteridofitas mexicanas, familia Dryopteridaceae*. M. Sc. thesis, Facultad de Ciencias, Universidad Nacional Autónoma de México, Mexico, D.F.

Mendoza-Ruiz, A. and B. Pérez-García. 2003. Comparative analysis of the sexual phase of *Phanerophlebia* (Dryopteridaceae) in Mexico. Can. J. Bot. 81:501–516.

Mendoza-Ruiz, A., B. Pérez-García and R. Riba. 1999a. Morfología yanatomía del gametofito de *Didymochlaena truncatula* (Dryopteridaceae). Rev. Biol. Trop. 47:87–93.

Mendoza-Ruiz, A., B. Pérez-García and R. riba. 1999b. Morfogénesis de la fase sexual del helecho *Arachniodes denticulata* (Dryopteridaceae). Rev. Biol. Trop. 47:791–797.

Mendoza-Ruiz, A., B. Pérez-García and R. Riba. 2002. Comparative research of gametophytes of *Olfersia alata* and *Olfersia cervina* (Dryopteridaceae). Amer. Fern J. 92:45–54.

Momose, S. 1937. Studies on the gametophytes of ferns. I. On the prothallial development and prothallium of *Dryopteris varia* O. Kuntze. J. Jap. Bot. 12:113–120.

Momose, S. 1939. Studies on the gametophytes of ferns. IX. Further observations on the prothallium of eudryopteroid ferns. J. Jap. Bot. 15:280–292.

Nayar, B. K. and S. Kaur. 1969. Type of prothallial development in homosporous ferns. Phytomorphology 19:179–188.

Nayar, B. K. and S. Kaur. 1971. Gametophytes of homosporous ferns. Bot. Rev. 37:295–396.

PÉREZ-GARCÍA, B., A. MENDOZA, J. I. REYES and R. RIBA. 1999. Morfogénesis de la fase sexual de seis especies mexicanas de helechos del género *Dryopteris* (Dryopteridaceae). Rev. Biol. Trop. 47:69–81.

PÉREZ-GARCÍA, B., A. MENDOZA, J. I. REYES and R. RIBA. 2001. Morfogénesis de la fase sexual de seis especies mexicanas del género *Dryopteris* (Dryopteridaceae), Parte II. Rev. Biol. Trop. 49:265–278.

TRYON, A. F. and B. LUGARDON. 1991. *Spores of the pteridophyta: surface, wall structure, and diversity based on electron microscope studies.* Springer Verlag, New York, USA.

TRYON, R. M. and A. F. TRYON. 1982. *Ferns and allied plants, with special reference to tropical America.* Springer Verlag, New York, USA.

ZHANG, K. M., L. SHI, X. C. ZHANG, C. D. JIANG and W. L. TIM-CHUN. 2008. Gametophyte morphology and development of six Chinese species of *Pteris* (Pteridaceae). Amer. Fern J. 98:33–41.